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Resolving when (and where) the Thylacine went extinct

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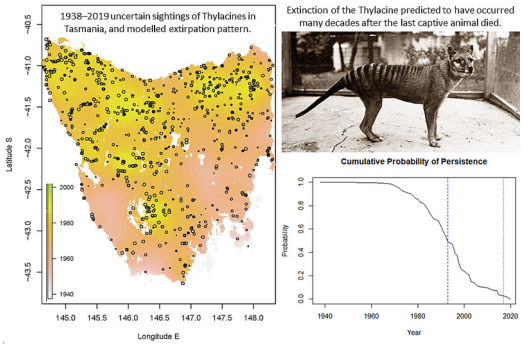
HIGHLIGHTS

- The Thylacine (Tasmanian Tiger) was famously thought to have gone extinct in 1936.
- We compiled an exhaustive record of later possible sightings to test this assertion.
- Using uncertainty modelling, we mapped the likely regional extirpation pattern.
- Contrary to the consensus, this iconic predator probably persisted until the 1980s.
- Our new spatial method will be useful for inferring any species' range contraction.

GRAPHICAL ABSTRACT


1938–2019 uncertain sightings of Thylacines in Tasmania, and modelled extirpation pattern.
Extinction of the Thylacine predicted to have occurred many decades after the last captive animal died.
Cumulative Probability of Persistence
Latitude S
Longitude E
Probability
Year

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ABSTRACT

Like the Dodo and Passenger Pigeon before it, the predatory marsupial Thylacine (*Thylacinus cynocephalus*), or 'Tasmanian tiger', has become an iconic symbol of anthropogenic extinction. The last captive animal died in 1936, but even today reports of the Thylacine's possible ongoing survival in remote regions of Tasmania are newsworthy and capture the public's imagination. Extirpated from mainland Australia in the mid-Holocene, the island of Tasmania became the species' final stronghold. Following European settlement in the 1800s, the Thylacine was relentlessly persecuted and pushed to the margins of its range, although many sightings were reported thereafter—even well beyond the 1930s. To gain a new depth of insight into the extinction of the Thylacine, we assembled an exhaustive database of 1237 observational records from Tasmania (from 1910 onwards), quantified their uncertainty, and charted the patterns these revealed. We also developed a new method to visualize the species' 20th-century spatio-temporal dynamics, to map potential post-bounty refugia and pinpoint the most-likely location of the final persisting subpopulation. A direct reading of the high-quality records (confirmed kills and captures, in combination with sightings by past Thylacine hunters and trappers, wildlife professionals and experienced bushmen) implies a most-likely extinction date within four decades following the last capture (i.e., 1940s to 1970s). However, uncertainty modelling of the entire sighting record, where each observation is assigned a probability and the whole dataset is then subject to a sensitivity analysis, suggests that extinction might have been as recent as the late 1980s to early 2000s, with a small chance of persistence in the remote south-western wilderness areas. Beyond the intrinsically fascinating problem of reconstructing the final fate of the Thylacine, the new spatio-temporal mapping of extirpation developed herein would also be useful for conservation prioritization and search efforts for other rare taxa of uncertain status.

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1. Introduction

Prior to European settlement in the early 1800s (Jeffreys, 1820), the large island of Tasmania supported an endemic population of a cursorial predator called the Thylacine (*Thylacinus cynocephalus*)—also known as the 'marsupial wolf' or 'Tasmanian tiger' (Guiler, 1985)—a species that had been extirpated on mainland Australia during the late Holocene, after surviving the earlier wave of late Pleistocene megafaunal extinctions (Prowse et al., 2014). The pre-colonial population size of Thylacines in Tasmania has been estimated to have been between 2000–4000 individuals (Guiler and Goddard, 1998), having co-existed with indigenous people there for 14,000 years after the island's isolation from mainland Australia at the end of the last ice age (Prowse et al., 2013). However, due to deliberate persecution from the 19th century onwards (encouraged by government and private bounties, paid out from 1888 to 1909), incidental snaring and trapping by fur traders, occasional capture for the zoo trade, habitat modification and possibly disease (Paddle, 2012), the Thylacine had declined to extreme rarity by the early 20th century. The final confirmed wild captures and kills of the species occurred in the 1930s (Sleightholme and Campbell, 2016). Recent modelling using annual sighting data has concluded that extinction occurred soon thereafter (Carlson et al., 2018).

The last captive Thylacine died in the Hobart Zoo on 7th September 1936, a date now commemorated annually as 'Threatened Species Day' in Australia. Fifty years later, in 1986, the species was formally designated as Extinct by the International Union for the Conservation of Nature. However, with many unconfirmed sightings reported in the decades after the 1930s (Rounsevell and Smith, 1982), speculation has run rife that the Thylacine might have persisted far longer than formally accepted in the wilderness of Tasmania (Drollette, 1996). Indeed, as one of the most famous of recently 'extinct' species, and an archetype of convergent evolution (with placental canids) (Owen, 2003), the details surrounding the final fate of the Thylacine in its last island stronghold is fascinating to both the public and conservation science (Bulte et al., 2003).

Complicating matters, apparently reliable sightings came from former trappers and bushmen through to the 1960s (after which most had long retired or died). Dedicated expeditions continued thereafter, including an intense localized search by authorities in 1982 following a highly rated sighting by a National Parks officer (Guiler and Godard, 1998). The regularity and frequency of apparently plausible but unverified sightings reported over the last 85 years has not only raised the Thylacine to iconic status in the global public's eye, but also made it paradoxically challenging to reconstruct the timeline of its fate scientifically. Past efforts to prove the ongoing persistence of the Thylacine involved deliberate and sustained (albeit geographically restricted) field searches (Griffith, 1972; Smith, 1981), with them sometimes being financially motivated (e.g., media mogul Ted Turner offered a prize of $100,000 in 1983, and *The Bulletin* magazine of $1.25 million in 2005). There are also psychological effects that can be important in these cases (e.g., framing and reference-point effects; see Iftekhar and Pannell, 2015). More recently, mathematical models have been used to estimate the extinction time, but the scope of their inferences have—to date—been hampered by lack of data, being based on a simplified sighting record (one observation per year) or using generalizations from life-history correlates and analogies with other taxa (Brook et al., 2018; Lee et al., 2017). Although statistical approaches for extinction inference using a time series of observational records have been developed to incorporate observational quality explicitly (Boakes et al., 2015; Kodikara et al., 2018), these could only be applied to the Thylacine's case in a highly constrained way (i.e., by designating each year as either a certain, uncertain or no record: Carlson et al., 2018), because the sighting data and the circumstances surrounding each reported incident had never been systematically collated or quality rated.

Given the inherent complexities and data constraints, what can be said, scientifically, about the extinction date of the Thylacine? To tackle this intriguing problem, we compiled a comprehensive, quality-rated database of post-government-bounty Thylacine sighting records from Tasmania and devised a spatio-temporal method to visualize its extinction dynamics. The sighting database was amassed by searching and cataloguing records from official government archives, published reports, museum collections, newspaper articles, microfilm, contemporary correspondence, private collections or other miscellaneous citations and testimony. Each observation was dated, geotagged, quality-rated, categorized by type, and linked to image files of the original source material. Only post-1910 records were considered, being the period following the cessation of the government bounty, after which the species was considered rare (Guiler, 1985). Records were classified as physical specimens, expert sightings, other observations, signs (e.g., tracks), and were all rigorously quality rated.

Using this curated sighting database, our goal was to evaluate alternative scenarios for the timing of extinction of the Thylacine and mapped the pattern of its preceding regional extirpations. To do this, we applied a recently published method for inferring the probability of persistence beyond that of the final record, under circumstances where many observations are uncertain but not equally reliable (Brook et al., 2019). Using a probabilistic re-sampling of sighting records, this provides an estimate of the timing of the last true observation of the species. We also combined this pre-processing method with two statistical extinction-date estimator (EDE) models: i) the optimal linear estimator (OLE), used for famous examples such as the Dodo (*Raphus cucullatus*) (Roberts and Solow, 2003), and ii) the variable-sighting-rate method (McInerny et al., 2006). Both EDE models are robust to cases where sighting frequency declines over time (Jarić and Roberts, 2014). Within this context, we considered a wide range of viewpoints and assumptions, from the conservative (i.e., rejection of all unverified records), to the liberal (i.e., use of all reported sightings, weighted by sighting quality). Our aim was not to determine precisely when (and where) the last Thylacine died, but to offer plausible scenarios.

2. Methods

The approach involved the following steps: (i) collation and georeferencing of Thylacine sighting records from Tasmania into a database of unique observations; (ii) error-checking, attribute scoring, and quality-rating; (iii) a scenario analysis, based on selective rejection of sighting records, to infer the island-wide distribution of times to extinction for the Thylacine; (iv) a sensitivity analysis on the impact on extinction time of different record-inclusion probabilities; and (v) dynamic distribution mapping, to illustrate the spatial patterns of extirpation.

2.1. Database compilation and validation

We compiled and error-checked a comprehensive repository of documented Thylacine sighting records from Tasmania, covering the period from the year after the last Government bounty was paid (1910) to the present. We refer to this as the Tasmanian Thylacine Sighting Records Database (TTSRD). By examining sources exhaustively, spanning official archives, published reports, past (partial) compilations of sighting records (Guiler, 1985; Rounsevell and Smith, 1982; Smith, 1981), museum collections, newspaper and media articles, microfilm, contemporary correspondence, private collections and other miscellaneous citations and testimony, we were able to amass 1237 unique observations from this period, as well as resolve previous anomalies and duplications.

The TTSRD is presented in a flat-file format (.xlsx or .csv), with one observation per row, and column data for a unique ID, sighting location (with notes), date (year/month [or season]), geo-reference (latitude/longitude and a precision class), sighting type (kill, capture, expert or non-expert visual observation, secondary evidence) and quality-rating (a score between 1 [lowest] to 5 [highest], based on a subjective composite of information regarding the observer's credentials and experience (e.g., whether the person had previously trapped Thylacines, or had worked in the Tasmanian bush and was familiar with the local wildlife, or was a transient visitor from elsewhere, etc., along with the number of human observers and detail of the description supplied). The quality scores were assigned by Dr. Stephen Sleightholme and Mr. Cameron Campbell, who are co-authors on this

paper. Stephen is one of the world's leading experts on the 19th to 20th century records of the Thylacine and compiled (and updates) the *International Thylacine Specimen Database*. Cameron created (in 1999) and curates the *Online Thylacine Museum*. They have co-published over a dozen refereed papers on the history of the Thylacine. Given that we are modelling a species that is now consigned to the past, these quality scores inevitably carry some burden of subjectivity. Nonetheless, it is difficult to imagine two more qualified authorities to make these judgements.

We also noted various other meta-data associated with the sighting, such as whether the observation was made along a road or in the bush, if the observer was driving or walking, if it was seen during the day or at night, the distance of the animal, being either near [<30 m] or far [>30 m], and the number of Thylacines seen, along with observer remarks and a reference and link to an image of its source material(s). Confidentiality requirements necessitated the redaction of names and addresses for 89 records, but efforts were made to prevent this censure affecting the essential content of the reports. The TTSRD was checked rigorously for repeated or erroneous entries (e.g., there were examples when the year or location did not exactly match, or when observer's names were misspelled, but other corroborating or correlative evidence pointed to a duplication). Any errors we found were archived and removed, with the record's unique ID not reused.

2.2. Extinction date estimation

Given the difficulties inherent in observing rare or critically endangered taxa, statistical methods (extinction dynamics estimators: EDE) have been developed to *infer* probable extinction dates (or, by inversion, probabilities of persistence) from a time series of sighting records. Recent approaches to EDE have sought to incorporate a mixture of certain and uncertain sighting records (Boakes et al., 2015). Both Bayesian (Kodikara et al., 2018; Solow and Beet, 2014) and frequentist (Brook et al., 2019; Jarić and Roberts, 2014) methods have been developed, each with advantages, limitations and differing philosophical framings of the problem.

In this analysis, because of the character of the data embodied within the TTSRD (see Results), we chose to use a recently developed pre-processing method for the inclusion and relative weighting of observations (Brook et al., 2019; Jarić and Roberts, 2014), implemented in Program R (v4.1). This approach is useful in this context because it can incorporate explicit sighting probabilities on uncertain data, multiple sightings within a year, and mixed records of variable type and quality. By using a weighted resampling method, it offers a simple yet powerful computational approach that incorporates observational reliability into EDEs. It does this by repeatedly sampling observations by using their reliability scores as an inclusion probability and then uses the resulting stochastic sighting-record vectors as input data for any EDE. When the sighting record is re-sampled repeatedly, this method can be used to infer a probability distribution, summary statistics and frequency distribution of extinction dates (Brook et al., 2019). One of the main strengths of the approach is that it estimates confidence bounds empirically (akin to a parametric bootstrap), and handles sighting uncertainty in the data pre-processing step, rather than as an assumption-driven characteristic of the EDE (e.g., Solow and Beet, 2014). The method is easy to implement with the optimized, parallelized R code provided to run the model (Brook, 2019). For detailed information about the method, see Brook et al. (2019) and its appendices.

With this approach, we can either use the sighting records directly to estimate the year of the last true observation (i.e., with no EDE), or apply EDEs (McInerny et al., 2006; Roberts and Solow, 2003) for statistical inference, after probabilistically sampling of the full sighting record, to generate a frequency distribution of extinction times, as demonstrated and validated using various example species records in Brook et al. (2019). We note that in this method, and indeed in all frequentist EDE models, the null hypothesis underlying the statistical inference is that of persistence. In a more nuanced way, every sighting is assigned a probability of being correct, given an assumption that the species persisted up to at least the point in time when the observation was made, rather than simply being accepted as true or rejected as unequivocally false. A detailed evaluation of the assumptions underpinning this approach, and the alternatives, are given in the Supporting Information, Appendix S2.

2.3. Scenarios and sensitivity analysis for the Thylacine's extinction

Our analysis is predicated, in large part, on assumptions about which records are true and which are false (whether from misidentification, illusion or deception). In terms of possible scenarios, the most conservative assumption is to accept only those records based on kills or captures, in which a body, a photograph of a body, or a live animal was produced, i.e., physical specimens. We first used standard EDEs to model these records, using either island-wide or regional collections. We then experimented with the remaining dataset of uncertain observations, to assess the impact of applying different inclusion/exclusion criteria, in concert with the probabilistic weightings, on the extinction-year estimate (the physical records are included in all other scenarios because they are certain and should never be rejected). For example, one possibility is to also include unconfirmed kills and captures (where a kill was reported but the body was left behind, or an animal was trapped but then released or it accidentally escaped during handling). Another is to set a plausibility threshold on uncertain sightings, accepting only those that meet rigorous quality standards, and rejecting all others, or to only consider sightings that were made by two or more witnesses. Similarly, a threshold could be applied to a date, by accepting records prior to a given year and rejecting those reported afterwards (in reality, after the true extinction year, all sightings are axiomatically false; however, this year is of course not known, a priori, being the variable under question). Finally, a mixed-certainty EDE could be applied, using some (e.g., only 'expert-rated' sightings), or all records, with each sighting assigned a probability of being true, and scenarios constructed based on different relative weightings. We tried examples of all these approaches herein, while acknowledging that there is essentially no limit to the alternative interactions and dependencies among assumptions that might be imagined.

A sensitivity analysis was also done on inferences made by the EDE-model-under-uncertainty using all records (reported in the Results), with additional variants, such as alternative record-weighting schemes, and alternative EDE parameterizations, reported in the Supporting Information, Appendix S5. Therein, Table S3 gives the relative probability (P) weightings of records by type (physical specimen, expert observation, expert indicator of presence, and other observations or indicators), for low (L), default (D) and high (H) weights, and Table S4 reports the probability multipliers on the weightings given in Table S3, which depend on the quality rating.

The probability of inclusion is ultimately all that the EDE inference model uses. The sighting type and quality scores simply provide for context-specific modifiers on this probability and allow the user to change these and thus create alternative sensitivity scenarios. To illustrate, the 'baseline' sighting probabilities (*sp*) are reported in Table S3, with the quality multipliers (*qm*) in Table S4. Assume use of the default (D) sighting-type probabilities column (Table S3, $sp = 0.25$) and that the sighting was EO (expert observation), with a quality rating of 3 (Table S4, $qm = 0.6$). Under this scenario, the final inclusion probability for a EO3 record is $0.25 \times 0.6 = 0.15$.

Table S5 shows the results of models applied to the extinction of the Thylacine in Tasmania, broken down by geographic region, when restricted to only physical specimens. Table S6 expands this to both physical specimens and expert-sighting records, and in Table S7, all available records.

2.4. Spatially continuous mapping of the extirpation pattern

Both the last capture and the last confirmed kill of a Thylacine in the wild were situated in a semi-agricultural region of north-west Tasmania (Sleightholme et al., 2020). However, many reports continued to come thereafter from more remote central and south-west regions of the island, a vast stretch of wilderness that was sparsely settled and relatively rarely

traversed or trapped. To create a visualization of the extirpation pattern and relax the 'hard-boundary' assumption inherent in the approach based on bioregional divisions (see Tables S5-S7), we developed a spatially continuous mapping method, implemented algorithmically in R. The input is a raster map of grid cells representing the landscape occupied by the species. In our case, we gridded the main island of Tasmania into 69,562 × 0.01° longitude-latitude cells (~ 0.92 km^2 at the Tasmanian latitudinal range of −40.65 to −43.64° S). For each grid cell, a subset of sighting records within a pre-defined radius are selected (we chose a threshold of 75 km for the Thylacine in Tasmania). Sighting records within that subset are then weighted for inclusion in the probabilistic EDE based on a distance-decay function. We used a truncated exponential model, $w = \min(1, ab^{-d})$, where $a = 2.15$, $b = 1.074$ and d is the distance (in km) from the target cell (other mathematical models could be used, if deemed more appropriate to a situation). These values were used because the model parameterized in this way led to a weighting (w) of 1 for all records within 10 km distance, declining to approximately 0.5 by 20 km, 0.25 by 30 km, 0.05 by 50 km, and 0.01 by 75 km, which is appropriate for what we know of the Thylacine's probable home range and dispersal patterns (Guiler, 1985). For use in the EDE, the w value of each record is multiplied by its sighting probability (see above, 'Extinction date estimation' section). Because of the large number of grid cells, we used the variable sighting rate EDE model (McInerny et al., 2006), because an analytical form of the under-record-selection-uncertainty framework has been derived (see Jarić and Roberts, 2014), making it more computationally efficient than the generalized (but slower) re-sampling approach. When iterated over all spatial-grid cells, this algorithm produces a final map of inferred extirpation times. For enhanced execution speed, the R code makes use of multi-core parallel processing. We also provide a sensitivity analysis of the distance-decay function, and time-sliced kernel-density map, as Figs. S1 and S2.

The obvious advantage of a spatially continuous approach is that it generates a smoothed geographic surface and contours of extirpation times that can be mapped, based on the inferred year of extinction or upper confidence bound, as derived from an EDE. Importantly, because the method makes use of all records within a defined radius (with their selection probability down-weighted monotonically by distance), it does not impose hard boundaries like in the discrete-bioregional approach and captures spatial-pattern information from both within and across the bioregions. Moreover, regions of high uncertainty (wide confidence bounds) are readily distinguished (and visualized) from those underpinned by more data and/or better-constrained inferences on extirpation. The main limitation is that the mathematic form (and parameter values) of the distance-decay function is ultimately subjective, yet these choices govern the degree of spatial smoothing apparent in the resultant probability map. Although the spatially continuous mapping algorithm was developed specifically for the Thylacine, the approach (and R code) is designed to be general and could be readily applied to other species with geo-referenced sighting records.

3. Results

3.1. Database metrics

The final database comprised 1237 entries (99 physical records, 429 expert sightings, 709 other sightings), with observations from all years except 1921, 2008 and 2013. Many records from 1910 to 1936 (the year the last captive specimen died—a male captured in 1931 (Sleightholme et al., 2020), see photograph in Fig. 2) were of confirmed kills or live captures, although 56.6 % (128) of the 226 entries dating from this period were unverified sightings. The last fully documented wild animal (with photographs) was shot in 1930, but there is little reason to doubt the legitimacy of two bodies noted from 1933, nor two other capture-and-releases from 1935 and 1937. Thereafter, over the course of eight decades, a further 26 deaths and 16 captures were reported (but not verified), along with 271 sightings by 'experts' (e.g., former trappers, bushmen, scientists, or officials). The other 698 sightings from Tasmania were made by the general public.

There were notable spikes in reporting rates in 1937 and 1970, the former following legal protection and the latter arising from media attention linked to a well-publicized expedition: these are examples of the framing and recency biases noted above (Iftekhar and Pannell, 2015). There are also many examples of discrete spatio-temporal sighting clusters with closely matching visual descriptions, the interrelationships of which would not have been apparent at the time the reports were submitted to authorities. Overall, the annual number of reports in the six decades spanning 1940–1999 were relatively constant ($\overline{x} = 14.9$ year^{-1}, $\sigma\overline{x} = 1.15$), but fell substantially ($\overline{x} = 3.6$ year^{-1}, $\sigma\overline{x} = 0.60$) from 2000–present. A breakdown of observations by type and quality, and time-series plots, are reported in the Supporting Information (Appendix S4).

Time-series plots of these data (Fig. 1) show a rise then fall in expert high-quality sightings over time, with a similar but lagged response for non-expert high-quality sightings, and a peak then a relatively constant rate for lower-quality sightings. Our interpretation of this pattern in the raw data is that extinction seems to have occurred sometime after 1985, when the frequencies decline for all types. Further to this point, within the TTSRD, there are 32 high-quality (S4/S5) sightings for the 1960s, 20 for the 1970s, 12 for the 1980s, 8 for the 1990s and 1 for the 2000s.

3.2. Range-wide extinction scenarios and sensitivity analysis

Restricting the EDE inference solely to the physical specimens results in an uncontroversial conclusion: extinction by 1941 (Table 1), with a regional east-to-west pattern of loss (Table S5). The physical records ceased earliest in the midlands and south-east of the island, which coincides with where human settlements and farming were most widespread in the early 20th century. If the uncertain kills and captures are also considered, the lower-bound for extinction is pushed out to the mid-1950s, with the median estimate spanning the 1970s to 1980s. If only the highest-quality uncertain sightings are included alongside the physical records, then the lower-bound is the late-1950s to early 1960s, with the median estimates spanning the late 1980s to 1990s (Table 1); similar results come from only considering sightings that were reported by multiple witnesses. Arbitrarily fixing a cut-off date does not seem helpful, because the sudden truncation of records causes both the last true record, and the EDE-inferred extinction, to fall within a year of the applied threshold, leading to a somewhat circular result.

Relaxing the constraints further, if all unverified expert reports are considered by down-weighting them proportionally according to their quality rating (as per Brook et al., 2019)—the projected extinction window spans a later period, from the 1980s to the present, although the probability of ongoing persistence to 2020 is low (Table 1; Fig. 2a,b). This might seem surprisingly recent, but is supported by, for example, the concerted official search efforts from Parks & Wildlife authorities in the 1980s that were motivated by apparently highly credible sightings (Smith, 1981). Finally, in the most liberal treatment of the sighting record, where all records, including opportunistic sightings by the public, are used, yields a similar conclusion. If low inclusion probabilities are assigned to each type of observation, then the extinction window spans 1969–2017 for the date of the last true observation, with a median estimated year of 1993.

A sensitivity analysis shows our results to be robust to permutations in the record-inclusion criteria or assignment of sighting probabilities (Fig. 2c and Appendix S5).

3.3. Pattern of extirpation across Tasmania

The Tasmania-wide aggregated analysis (Table 1, Fig. 2) combines sighting records of the Thylacine from across the island, irrespective of location. However, extinction often progresses via an intermediate process of range contractions and spatially heterogenous declines, themselves driven by a variable local intensity of threats like habitat change and hunting. Fig. 3 shows the inferred pattern of extirpation mapped as a geographical projection of point-wise extinction-date estimates on a 0.1° latitude-longitude grid, with the contribution of sighting records

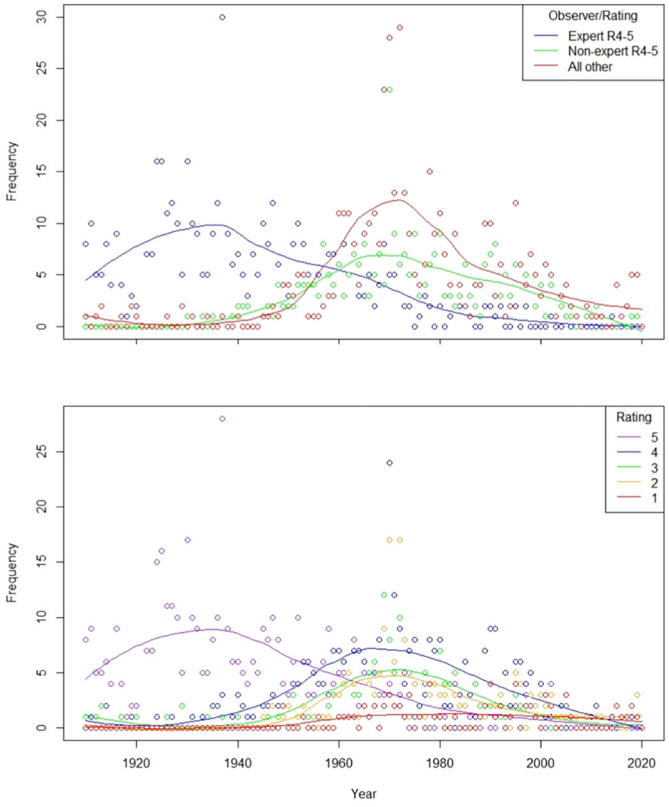

Fig. 1. Time series of Thylacine sightings in Tasmania, tallied by year, from 1910 through to 2019. The upper panel shows a quality breakdown of sightings (rating 4–5), separated into experts (blue dots) and non-experts (green), and compared to all other (lower-quality) sightings, rated 1–3 (red). The lower panel is based solely on quality rating, from 5 (highest) to 1 (lowest). The lines are *loess* fits (local polynomial regression smoother, with span = 0.75 and degree = 2).

surrounding each landscape-grid point down-weighted using a distance-decay function, while retaining each record's respective sighting probability. These multi-weighted contour surfaces, superimposed on a coastal outline of Tasmania, reveal a general pattern of local losses starting in south-east and midland regions of the island (abutting areas where grazing, agriculture and settlement was concentrated) and later extending to the remote wilderness areas of the center and south-west.

The situation for the species by 1937 (based on a mixture of records on kills, captures and expert sightings) was of a severe decline across most of the landscape, with pockets of probable persistence in south-central and north-west regions of the island, likely connected by dispersal corridors (Fig. 3a,b). There was also some possibility of a remnant isolated sub-population persisting in the north-east at that time, but with strong evidence for an early extirpation (by the 1920s) in the midlands and along the south-east coastal region, where the bounty killing had been particularly intensive (Prowse et al., 2013). From 1938 onwards, all records (through to 2019) are of unverified sightings or reported (but not confirmed) kills and captures, of varying quality, coming from experienced trappers through to the (largely) Thylacine-naïve public. These data (Fig. 3c,d) indicate extirpation by the early 1960s across most of the southern half of the state, with longer-term persistence along a band stretching across the Tasmanian Wilderness World Heritage Area, from Lake Pedder in the south-center across to the western edge of the central highlands and up to the Tarkine in the north-west. There is also remarkable congruency across the two sets of extirpation maps in the geographic location of potential refugia ('hotspots' of records), despite being based on assessment of completely temporally separate, non-overlapping data (the latter period has no certain, verified records). The most likely termination date for the species seems to have occurred within this zone by the late 1990s, although the upper confidence bounds of the model include the present day in some wilderness regions of the island.

4. Discussion

Based on the extensive (albeit uncertain) sighting record that post-dates the death of the last captive Thylacine in 1936—which we integrated using spatially explicit inferential methods that account for mixed-quality observations—it seems reasonable to conclude that a remnant population of the species persisted in remote areas of Tasmania for many years thereafter. This assertion has been argued on other ecological and detectability grounds (Bulte et al., 2003; Guiler and Godard, 1998; Lang, 2014; Sleightholme and Campbell, 2016; Terry, 2005), however ours is the most comprehensive assimilation, model-based quantification, and spatio-temporal visualization of the full body of Thylacine sighting data. But why then, if the species persisted for decades after the 1930s, did the supply of live specimens and carcasses cease and, moreover, why was the species never photographed in the wild or confirmed by other scientific field methods?

The fate of the last wild individual of a species is rarely witnessed by people. This is especially true for species like the Thylacine, which ranged widely but sparsely across large swathes of the Tasmanian wilderness (Sleightholme and Campbell, 2016). The last survivors were probably increasingly difficult to detect as they became ever more wary of potentially fatal interactions with people, as numbers dwindled, and as the species' spatial distribution contracted and disaggregated as the species' population decline progressed (Fisher and Blomberg, 2011; Guiler and Godard, 1998). A

Table 1
Scenarios for the date of extinction of the Thylacine in Tasmania.

Scenario	n	No EDE model applied			Optimal Linear Estimator EDE		
		MTE	95 % CI	PE	MTE	95 % CI	PE
Physical specimens only (P)	99	1937	1934–1937	1	1939	1935–1940	1
P + unconfirmed kills/captures	162	1975	1953–1998	1	1986	1957–2019	0.975
P + multiple sighting witnesses	130	1986	1965–2009	1	1990	1969–2018	0.977
P + only highest-rated sightings	312	1995	1980–2002	1	1996	1981–2004	1
P + uncertain until 1950 cut-off	376	1951	1948–1950	1	1951	1949–1951	1
P + all 'expert' sightings (E)	429	2001	1986–2014	1	2006	1987–2023	0.806
All records (default weights)	1237	2011	1997–2019	1	2016	1999–2026	0.598
All records (low weights)	1237	1993	1969–2017	1	2007	1975–2040	0.834

Footnotes. Assessment using an aggregate of Thylacine records from 1910 to 2019, based on various combinations of verified physical specimens only, physical records and the addition of unconfirmed kills and captures, or all unverified expert sightings, or all record types (including physical records, expert sightings, and other observations by the public), weighted by the record's quality rating using default or low assigned probabilities. Shown for each scenario is the number of records sampled (n), mean time of extinction (MTE, calendar year) and the 95 % confidence intervals of the simulations (95 % CI, based on distribution percentiles), and PE shows the modelled probability of extinction in the year 2020 (Brook et al., 2019). Two methods are shown: a conservative approach wherein only probabilistic sighting-record resampling and no extinction-date-estimator model applied (no EDE); and alternatively, the results using the optimal linear estimator of Roberts and Solow (2003).

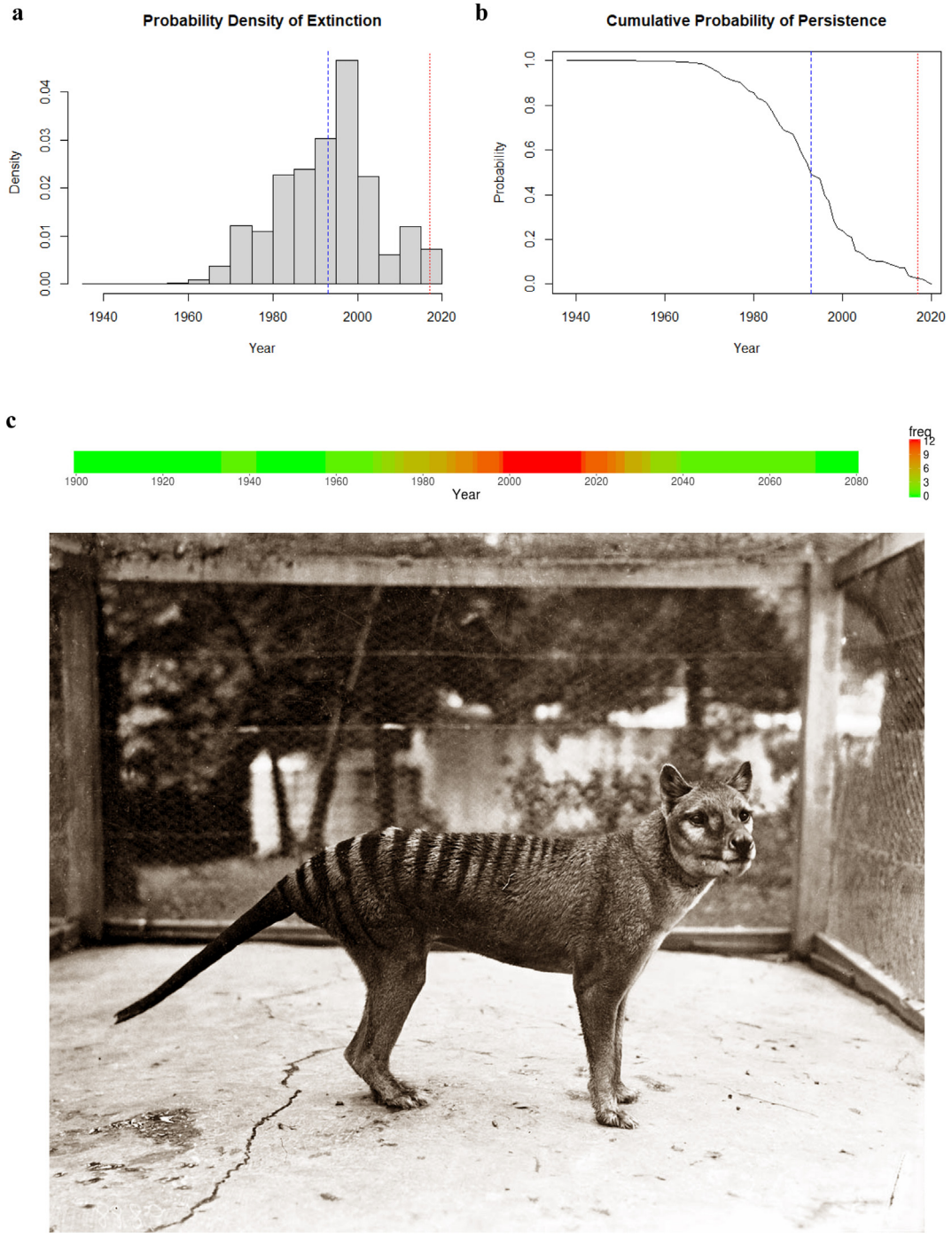

Fig. 2. Simulated extinction dates for the Thylacine in Tasmania, using all 1237 quality-rated sighting records. a. Probability-density distribution of the inferred last true sighting record, based on probabilistic re-sampling of all 1237 specimens and observations from 1910 to 2019, with the low scenario for probability weightings on the uncertain records. b. The inferred cumulative probability of persistence at a given calendar year, as derived from the distribution shown in a. In each panel, the blue and red vertical lines show the mean time of extinction and upper 95 % confidence bound, respectively. c. Sensitivity heatmap, using the optimal linear estimator extinction-date estimator, being a merger of upper/lower-bound weights assigned to sighting-type probabilities (default/conservative): physical records = 1/1, expert observations = 0.25/0.05, expert indications (e.g., footprints, scats) = 0.1/0.01, other observations = 0.05/0.005, other indications = 0.01/0.001. Photograph is of the last captive Thylacine, taken on 19th December 1933 at the Hobart Zoo by zoologist David Fleay (image courtesy David Fleay trustees).

direct reading of the physical evidence implies extinction in the wild by the mid-1930s. However, when species are driven to extreme rarity, most of the final records will be uncertain/unverified sightings; in the case of the Thylacine, after formal legal protection in 1936, there was a disincentive to self-report kills, for fear of penalty or prosecution (Brook et al., 2018).

Regarding verified detections, modern remotely triggered instruments are among the most cost-effective, unobtrusive and failsafe ways to record elusive vertebrate wildlife, and well-disguised cameras have been used to rediscover cautious carnivores that were previously thought extinct, such as the Zanzibar leopard (*Panthera pardus adersi*) (Goldman and Walsh,

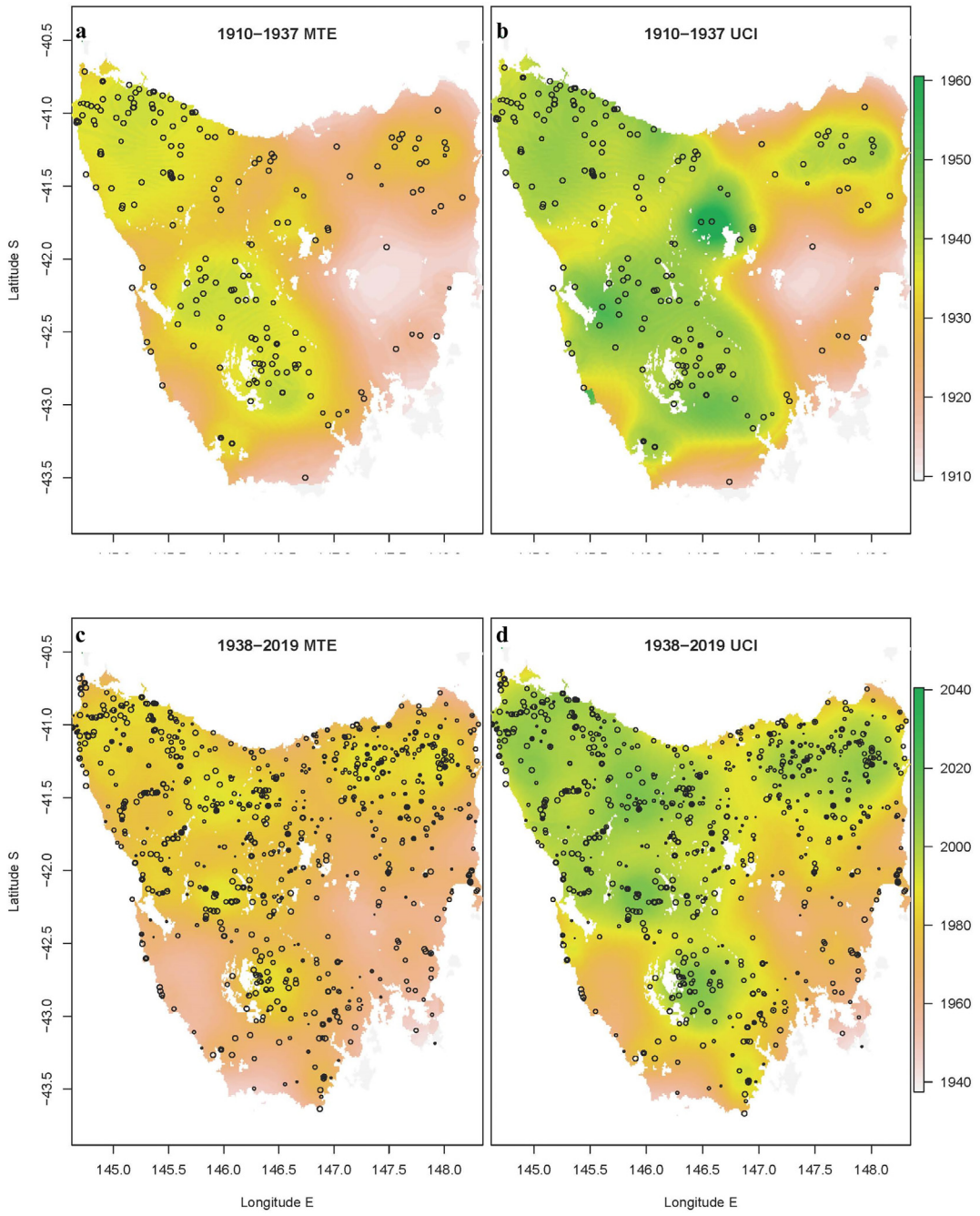

Fig. 3. Spatial extirpation pattern for the Thylacine in Tasmania. Colored contour maps of the inferred year of local extirpation, estimated for each pixel across a 0.1° geographical grid of the island (area = 64,519 km^2). The results were generated by fitting a re-sampled (Brook et al., 2019) variable sighting rate extinction-date estimator (McInerny et al., 2006) to the observational record, with sightings down-weighted by their assigned uncertainty and the great-circle distance from the target grid cell (see Methods). a. mean time of extinction (MTE) and b. upper confidence interval (UCI) for records spanning 1910–1937 (a mix of verified and uncertain records, n = 258). c., d., as for a., b., except using only records from 1938 onwards (all uncertain records, n = 979). The circles in each plot show individual sightings, sized by rated quality: 5 (highest quality) for the largest circles, down to 1 (lowest) for the smallest.

2002; Li, 2018). However, digital-trail-camera technology has only been widely deployed in field ecology over the past two decades (Meek et al., 2015), with earlier visual searches and film-camera field operations being of relatively short duration and restricted geographical coverage (Griffith, 1972; Guiler, 1966; Smith, 1981). Similarly, from the public's perspective, it has only been during this recent time span that smartphones and vehicle dashboard cameras have been in widespread use.

Although the extinction-range estimates reported herein span a more recent period than the estimate (1936–1943) derived previously from a Bayesian model of mixed-certainty sightings (Carlson et al., 2018), we have criticized the latter for only using a small fraction (<10 %) of all possible records (Brook et al., 2018). The Bayesian approach, when used on annually aggregated data, is insensitive to information embodied in the uncertain sightings, at least for the Thylacine, with only 1–3 years difference in the extinction-date estimate derived after rejecting all uncertain records, compared to modelling certain and uncertain records separately (Brook et al., 2018).

The most vexing difficulty with a scientific mystery like this—trying to decide which sightings are correct, and which are false—is quantifying the risk of ascertainment bias. During the post-bounty period, Thylacine

encounters were noted as being rare, but because there were still occasional kills and captures, the species was known with certainty to persist. During this time, unverified sightings were made regularly (128 reports between 1910 and 1936), and there seems little reason to doubt their authenticity, there being no general perception at the time that an unproven sighting was anything particularly remarkable (Sleightholme and Campbell, 2016). However, in the years following the death of the last captive Thylacine, when zoos sought new specimens (offering substantial remuneration) and yet none could be secured, interest in proving the species' ongoing existence steadily rose, such that by the 1960s it was recognized as a puzzling quandary (Griffith, 1972; Guiler, 1966). As recognition of this evidence gap grew, there was a greater incentive to falsely report sightings (for notoriety), or even a subconscious desire to *want* to see a live Thylacine, leading to inflated misidentification errors. Without the reassurance of an occasional 'ironclad' (physical) record, the time point at which there was a switch from some sightings being true, to *all* being wrong (i.e., after extinction), is left inevitably shrouded in the conservation-biology equivalent of a 'fog of war'. To try and cut through this, we are left with an inescapable reliance on observer credibility and the associated sighting details (much as is done when weighing up the usefulness of eyewitness testimonies in law courts; Wechsler et al., 2015), the specifics of which are listed for each record in the multivariate meta-data of the TTSRD. An extended discussion of this topic is given in Appendix S2 (Supporting Information).

Regardless of which scenarios or assumptions one chooses to favor or discount, our new method for mapping spatial contours of extirpation dates is useful not only for reconstructing the dynamics of the Thylacine's range contraction, but also for identifying the most likely spatial refugia occupied by the species prior to its range-wide extinction. Indeed, the extirpation-mapping algorithm we developed for the Thylacine case study is general and could be applied equally to other species of conservation concern that are verified to survive but where the synthesis of sighting records (confirmed or uncertain) has previously defied integration. Declining species with well-documented records of their range contraction might also be used to validate the model or provide more robust empirical estimates of the distance-decay-function. Additionally, these extirpation-probability maps could be unified with existing habitat- and climate- envelope methods (using occurrences recorded prior to a species' decline), to pinpoint regions where both available niche space and recent sightings indicate localities of potential survival, as a means of targeting more intensified search efforts, restoration, rewilding, or reallocation of resources when persistence is extremely unlikely (Rout et al., 2010).

In conclusion, this collective body of evidence and associated analyses indicates that while the Thylacine is unlikely to persist to the present, the true extinction year likely occurred much later than the commonly held date of 1936, when the last captive animal died. Indeed, our scenario analysis on new sighting-record compilation implies that the inferred island-wide 'extinction window' is wider and more recent than suggested by previous modelling (Carlson et al., 2018), spanning from the 1960s to the present day, with the peak likelihood centered on the late 1980s to early 2000s. Certainly, these aggregate data and modelling point to the species persisting within the remote wilderness of the southwest and central highlands regions of island for decades after the last confirmed specimen. Finally, we note that although our findings for this iconic species hold intrinsic value, our new spatio-temporal mapping of extirpation patterns is also applicable more generally, to support the conservation prioritization and search efforts for other rare taxa of uncertain status (Jarić and Roberts, 2014; Solow, 1993; Solow and Beet, 2014).

CRediT authorship contribution statement

B.W.B., S.R.S., C.R.C. and J.C.B. conceived the project and developed the database, B.W.B. analyzed the data and wrote the paper, B.W.B., I.J. and J.C.B. created the display items. All authors discussed the structure, results, and interpretation, and commented on the manuscript. Authors declare no competing interests. The data supporting the results will be archived in an approved public repository with a data DOI. The code is hosted at github.com/bwbrook/ttsrd

Data availability

Data analysis and modelling were implemented in Program R v.4.0.2 (http://r-project.org). The source instruction code, functions and input data files required to reproduce all results reported herein are publicly available on GitHub (https://github.com/BWBrook/ttsrd), along with The Tasmanian Thylacine Sighting Records Database (TTSRD) as CSV file or a Microsoft Excel workbook, and images (attachments).

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

Extended discussion on the historical context of thylacine sightings (Appendix S1) and a critical analysis on what the TTSRD compilation can (and cannot) tell us about the Thylacine's extinction, given the limits of knowledge and inference (Appendix S2), along with a discussion on the bioregional patterns in the historical sighting records (Appendix S3). Supporting references are listed in Appendix S4, and Appendix S5 provides Tables S1-S7, giving detailed breakdowns of the TTSRD records by type, quality, sighting class, probability assignments, and regional scenario analysis for specific EDE models. Supplementary data to this article can be found online at doi:https://doi.org/10.1016/j.scitotenv.2023.162878.

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